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Branches of a twisting tree: Domain-specific threat psychologies derive from shared mechanisms

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Threat intensifies ideological investment (e.g., ethnocentrism, religiosity) as well as a diverse and orthogonally related set of responses, such as aesthetic preferences or tendencies to seek physical proximity with others. An emerging consensus unifies these diverse threat-responses as superficially varied expressions of a single underlying process designed to reduce anxiety. In contrast, evolutionary thinking favors hypothesizing multiple functions designed to strategically manage specific threats (e.g., pathogen threats should motivate responses targeted to deter contagion), and views anxiety as a proximate tool rather than an ultimate problem. As distinct threat adaptations co-opt proximate mechanisms related to anxiety, focusing on anxiety-reduction risks obscuring important functional differences. Here, current accounts of threatmodulated bias are evaluated through an evolutionary functional lens.

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The odds are that, within several decades at best, your heart will stop. Before dying, you will suffer infectious diseases, often acquired through pathogen-transmission events beyond your personal control. At times, you will find yourself isolated and uncertain, perhaps lost in an unfamiliar city or mired in a troubled relationship. You may even be physically assaulted. While one hopes that many years elapse before you actually face such calamities, research indicates that merely having imagined them — just now — may influence you in surprising ways.

Over the past 25 years, social psychologists have compiled extensive evidence that threat cues (e.g., of death, isolation, disease, violence, or confusion) can mobilize investment in ethnocentric, political, and religious values, as well as responses that are unrelated or indirectly related to

ideology [1–3]. For example, briefly contemplating death can lead judges to set higher bonds for alleged prostitutes [4], picturing the unraveling of a valued relationship can heighten religious commitment [5], and reading about disease can increase preferences for physical attractiveness [6]. Some responses appear specific to particular threats, whereas others (e.g., intensified group chauvinism) have been documented to follow numerous manipulations [1,3]. Although debate continues over which threat management account most parsimoniously encompasses all observations, the prevailing approaches in social and personality psychology agree that the function of threat-induced bias is to allay anxiety of one kind or another (see Table 1) [2,3].

Evolutionary perspectives, by contrast, conceptualize threat-induced biases as functional strategies to neutralize threats. Anxiety, on this view, is a proximate means of regulating cognitive and behavioral responses, not an ultimate problem. As unique problem-features distinguish varieties of threat, an evolutionary approach implies multiple content-dedicated systems rather than any single function [7*]. Importantly, specialized threat systems should derive from an efficiently shared neurocognitive substrate, as mental functions arise via modification of existing structures [8*,9**]. Appreciating that domain-specific threat systems draw on common mechanisms, and therefore share family resemblances, may help to resolve disputes over the general versus specialized function(s) of threat-responses.

Domain-general accounts and fluid compensation

The meaning maintenance model (MMM) frames threatbiases as attempts to cope with the anxiety elicited by any inconsistency between experience and expectation [2,10]. Within the MMM, 'meaning violations' encompass anxiety-eliciting perceptual anomalies, unexpected outcomes, or overt threats [11]. The reactive approach motivation model (RAM) similarly posits that the anxiety evoked when goals are threatened problematically inhibits functioning [12,13]. According to both approaches, anxiety is palliated by activating the behavioral approach system thought to mediate all goal-directed activities including the affirmation of cherished convictions [3,11]. Illustrative of the generality of the cues that can elicit ideological bias, MMM investigators have shown that exposure to surrealism, subliminal nonsense phrases, or change blindness can intensify the financial punishment of a prostitute [14–16], and RAM researchers have shown

Theoretical perspectives relating threat to response biases.				
Theoretical approach	Proposed elicitor	Proposed response	Proposed function	Reference
Meaning maintenance model	Any inconsistency	Fluid compensation	Palliate anxiety	[10]
Reactive approach motivation	Threat to valued goal	Fluid compensation	Palliate anxiety	[12]
Compensatory control theory	Lack of control/order	Affirm control/order	Palliate control/order anxiety	[39]
Group-based control theory	Lack of control	Affirm group identity	Palliate control anxiety	[42]
Terror management theory	Death cues	Affirm values	Palliate death anxiety	[43]
Unconscious vigilance	Subtle affective cue	Affective sensitization	Attend to hazards/resources	[1]
Coalitional psychology	Need for group aid	Signal group affiliation	Bolster social support	[36]
Behavioral immune system	Pathogen cues	Pathogen aversion	Avoid contagion	[46]

that undergraduate students manipulated to feel insecure about their intellect or valued relationships report more fervent religiosity [12], among other examples [3]. The ostensible interchangeability of threats and biases is often termed *fluid compensation*: anxiety-eliciting stimuli prompt anxiety-reducing responses, and content domains are only relevant inasmuch as individual, contextual, and sociocultural factors modulate the degree of anxiety or compensatory well-being that they engender [11,17].

Contrary to the MMM and RAM emphasis on anxietyreduction via arbitrary approach, some putatively fluid outcomes appear strategic. For instance, threat primes related to death [18] or valued relationships [12] intensify inclinations to consume food and other material resources, consistent with facultative shifting toward future-discounting strategies when future prospects are uncertain. A future-discounting interpretation appears particularly illuminative of responses to cues of physical hazard, as death primes lead individuals to accept smaller short-term rewards over larger future rewards, to pursue riskier financial strategies [19], and to desire earlier procreation [20,21]. These preferences also track the number of close bereavements individuals have actually experienced [22°]. Notably, these findings bear out directional hypotheses concerning adaptive behavioral responses to risky environments that are unrelated to putative benefits of anxiety-reduction.

Fluid compensation or neural co-optation? At the mechanistic level, proponents of fluid compensation often highlight observations of comparable brain reactivity to diverse sorts of threat [2,3,11,17]. The amygdala and the anterior cingulate cortex have received particular attention because they are responsive to a wide array of threatening or anomalous stimuli [23], including reminders of death [24]. The recurrent activation of these regions in diverse contexts is not surprising as they are embedded in circuits subserving widely varying functional behavior (e.g., thirst, child protection) [25,26]. Distinct threat-response systems should be expected to share neurocognitive structures as selection derives new mental functions by co-opting and elaborating existing structures

[7°,8°,9°°,27°]. For example, the dorsal anterior cingulate cortex and anterior insula appear important for representing the distress associated with both social isolation and physical pain, but physical pain also activates the posterior insula and somatosensory cortices [28], suggesting that subcomponents of the pain system were re-purposed to represent isolation. Future initiatives to individuate threat systems against their backdrop of shared neurocognitive architecture may examine the differential involvement of areas associated with components unique to particular threats, such as the representation of uncertainty [29], or, in the cases of social threats that strongly involve others' perspectives, the 'Theory of Mind' network [30].

The degree of fluid interchangeability reputed to characterize threats and biases is probably inflated, as qualitatively different judgments (e.g., derogating immigrants versus financially penalizing prostitutes) are frequently treated as equivalent measures of 'worldview defense' or 'value-affirmation'. This conflation obscures whether threats exert greater influence on thematically related versus unrelated judgments. Nevertheless, in addition to strategic functional responses, incidental responses may be expected insofar as activating the neurocognitive architecture related to threats of one type potentiates circuits relevant to others as a side-effect of co-optation. Such collateral activation may generate patterns consistent with fluid compensation in some circumstances, but more aptly characterized as 'glitch' interactions between domain-specific processes than as evidence of a single process. By the same token, dampening mutually co-opted mechanisms should reduce responsivity in distinct functional systems. For example, down-regulating dorsal anterior cingulate reactivity via acetaminophen administration reduces physical pain, isolation distress [28], and ideological biases following primes of death or randomness [31].

Many fluid effects follow subliminal primes, or subtle manipulations with distraction and delay [1,3]. These methods may evoke a state of 'alarm' which, though relatively undifferentiated, complements domain-specific threat responses. Unconsciously detected threats can

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